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Permian Scallops of the Pectinacean Family Streblochondriidae

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ABSTRACT

Permian scallops of the genera *Streblochondria* and *Guizhoupecten,* family Streblochondriidae, are here revised with the aid of superb collections of silicified specimens from western Texas. The more specialized of the two genera, *Guizhoupecten,* shares several "derived" characters with the post-Paleozoic family Pectinidae. This study illustrates the necessity of large, well-preserved collections for evaluating variable populations. Phylogenetic and ecological conclusions are deferred until we can properly document associated taxa.

INTRODUCTION

This is a further contribution to a monographic revision of those Pectinacea (scallops and near relatives) involved in the great Permo-Triassic mass extinction and subsequent replacement when the biosphere suffered an enigmatic shock (Newell, 1967, 1982).

Our intention is to make a comprehensive study of representatives of pertinent families and their dozens of genera. The project is centered on magnificent collections of silicified specimens belonging to the U.S. National Museum of Natural History and the American Museum of Natural History. The fossils were collected mainly from Permian reef complexes of West Texas (Cooper and Grant, 1972, pp. 1-8; Newell et al., 1953) supplemented by new collections made by us from Permian and Lower Triassic rocks of the Great Basin and the Rocky Mountains, and other materials borrowed from various institutions.

Our first contribution on the pectinaceans (Newell and Boyd, 1970) covered the oyster-like cemented species. The reader is referred to that publication for general orientation, comparative anatomy, and discussion of major adaptations within the superfamily Pec-

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TABLE 1
Measurements of Four Specimens of *Streblochondria sculptilis* (Miller)[a]

	—[b]	—[c]	—[d]	—[e]
H	44	21.50	—	33
L	39	18.50	21	29
H/L	1.13	1.16	—	1.14
C	7	3.5	—	—
C/L	0.18	0.18	—	—
Hi	22	11	16.5	17
Hi/L	0.56	0.59	0.79	0.31
A	13.5	8.5	10	10
A/Hi	0.61	0.55	0.61	0.48

[a] Explanation: L, length; H, height; C, convexity; Hi, hinge length; A, anterior ear; linear measurements in millimeters.

[b] USNM cat. no. 388868, loc. 702, right valve, Permian.

[c] USNM cat. no. 388868, loc. 702, left valve, Permian.

[d] USNM cat. no. 388869, loc. 722G, right valve, Permian.

[e] Cincinnati Univ. Museum cat. no. 3894, holotype, right valve, Pennsylvanian.

tinacea. We have also issued two papers on the distinctive shell microstructure exhibited by our fossils (Boyd and Newell, 1985; Newell and Boyd, 1985).

The present paper covers a single family of the Pectinacea, the Upper Paleozoic Streblochondriidae, elevated here from the subfamily Streblochondriinae Newell, 1938.

One of the genera (*Guizhoupecten*) shares a number of traits with the more primitive Aviculopectinidae and with the more specialized post-Paleozoic Pectinidae, suggesting a phylogenetic connection between the two. However, there are many genera yet to be included in this study, several of them unnamed. Consequently, we are deferring general conclusions about phylogeny and environments until the survey is completed.

ACKNOWLEDGMENTS

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DESCRIPTIONS

FAMILY STREBLOCHONDRIIDAE NEWELL, 1938
(Emended herein from STREBLOCHONDRIINAE NEWELL, 1938)

DIAGNOSIS: Upright to slightly procrescent, ovate, nearly equivalve, smooth or ornamented shells with a short hinge and small, subquadrate to obtuse, posterior ear; hinge plate supported by a buttress on each side of the resilifer; resilifer short, extended slightly forward; outer shell-layer radially fibrous in both valves (fig. 1).

RANGE: L. Carboniferous through Permian.

GENUS *STREBLOCHONDRIA* NEWELL, 1938

TYPE SPECIES: By original designation *Aviculopecten sculptilis* Miller, 1891.

DIAGNOSIS: Costellate or cancellate Streblochondriidae of low convexity.

RANGE: Lower Carboniferous through the Permian.

Streblochondria sculptilis (Miller)
Figures 1.1, 1.2a, 1.2b; table 1

Aviculopecten sculptilis, S. Miller, 1891. Indiana Geol. Survey, Advance Sheets 17th Annual Report, p. 92, pl. 20, fig. 5.

Streblochondria sculptilis, N. D. Newell, 1938 ("1937"). Kansas Geol. Survey, vol. 10, p. 82, pl. 16.

DIAGNOSIS: The shell is a little higher than long in a ratio of 1.1/1–1.2/1 with 60–70 slender ribs on both valves mainly in two ranks of alternating size, the smaller ones intercalated in early growth at a shell height usually less than about 10 mm; regular concentric fila cross the ribs to produce a cancellated

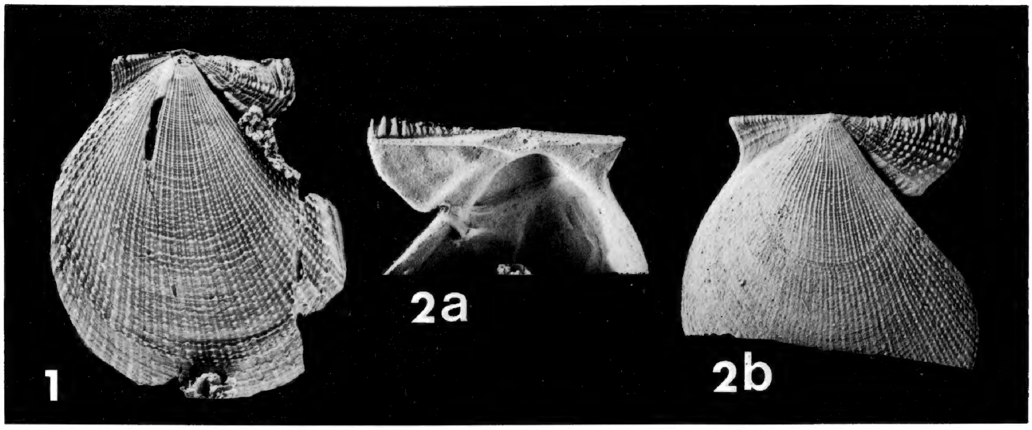

FIG. 1. *Streblochondria sculptilis* (Miller). **1.** Right valve, ×1. Cathedral Mountain Formation (Leonardian). USNM loc. 702, USNM cat. no. 388868. **2a, 2b.** Another right valve, showing the hinge. Road Canyon Limestone (Leonardian). USNM loc. 722 G, USNM cat. no. 388869.

pattern, with tiny scales at the intersections, especially marked on the anterior and posterior areas of the disk; hinge margin about one-half to three-quarters the length of the shell; anterior ear long, about one-half to three-fifths the length of the hinge.

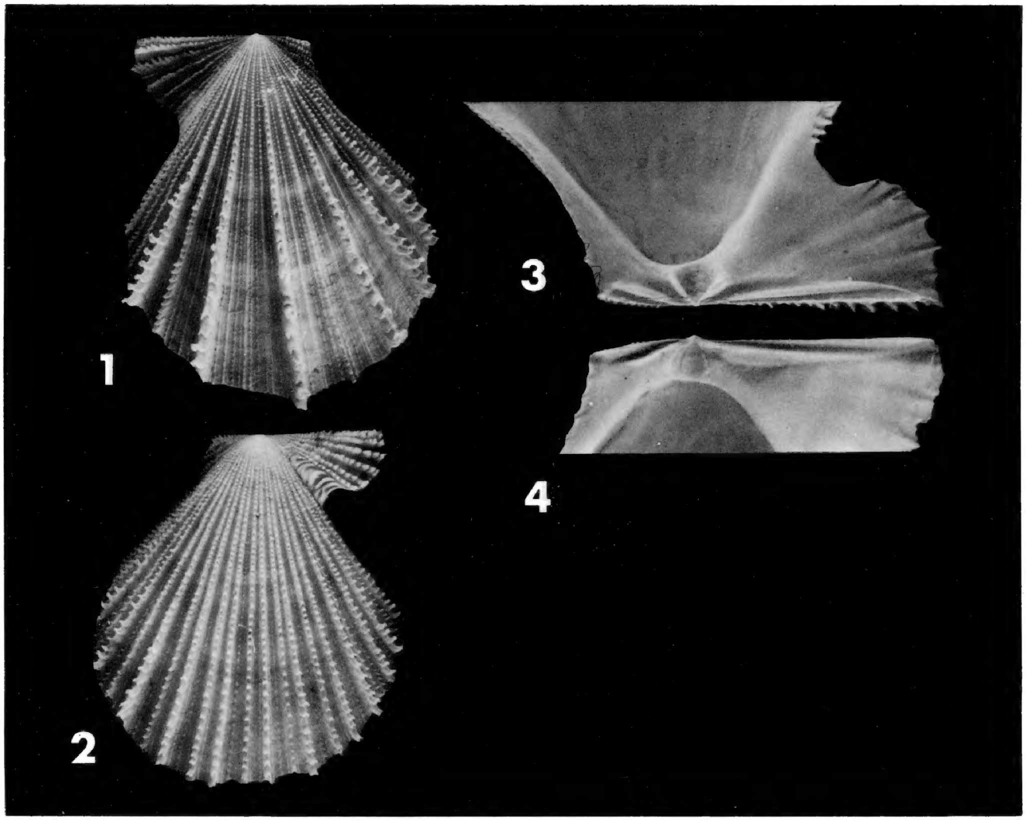

FIG. 2. *Chlamys hastatus* (Sowerby), Recent, Newport, Calif. AMNH Invertebrate Collection, cat. no. 206170. Matched valves, illustrated for comparison with Permian *Guizhoupecten*. **1.** Left valve, ×2. **2.** Right valve, ×2. **3, 4.** Same, hinge enlarged, ×4, right valve below.

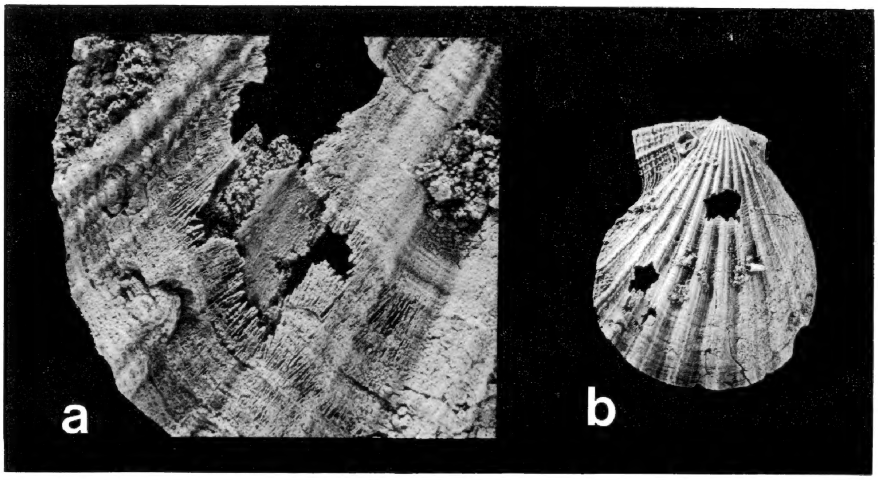

FIG. 3. *Guizhoupecten cheni,* Newell and Boyd, new species. A left valve showing details of fibrous structure. Lower Getaway Limestone, Middle Guadalupian, West Texas. USNM loc. 728 (same loc. as AMNH loc. 512). USNM cat. no. 382760. **a.** Approximately ×8. **b.** Same, ×1.

DISTRIBUTION: Upper Pennsylvanian to Lower Permian, inclusive.

DISCUSSION: Pennsylvanian occurrences have been cited by Newell (1938). The Permian examples before us include a hundred or so fragments of silicified shells, mostly left valves. They are abundant only at a single locality in the Bone Spring Formation (Leonardian), West Texas (USNM loc. 728f and AMNH loc. 629). Other silicified examples were collected from West Texas limestones ranging through the sequence from Wolfcampian into the lower Capitanian.

Appreciable variation is apparent but the material at hand does not permit statistical analysis.

The ornamentation is comparatively weak at the Bone Spring locality even though the shells are unworn. There are also erratic variations in convexity which may be correlated with different microhabitats in and around the ancient reefs of the area.

From the sparse material available we can find no significant difference between the Pennsylvanian and Permian forms.

GENUS *GUIZHOUPECTEN* CHEN, 1962

TYPE SPECIES: *Guizhoupecten wangi* Chen, 1962. By original designation. Upper Permian of China.

DIAGNOSIS: Shell ovoid, upright, nearly equilateral to slightly procrescent (opisthocline) with relatively convex disk, marginally plicate; beaks about two-thirds behind the front of a short hinge; ears subangular, posterior ear small, subquadrate; resilifer extending two-thirds of its length ahead of the beaks, and in juveniles the left valve resilifer is bounded on both sides by a single cardinal crus, above which articulates the ventral margin of the right valve (fig. 4.1a). A few right valves have a weak lower crus on the anterior ear (fig. 4.2a). The crura disappear in specimens more than 15 or 20 mm high.

DISCUSSION: In general aspect, this genus resembles species of the geologically younger pectinid *Chlamys* (fig. 2), from which it differs in the characters of the hinge and shell microstructure. The possession of primitive cardinal crura and the pectinid aspect of *Guizhoupecten* suggest an evolutionary grade in advance of most Paleozoic pectinoids.

RANGE: *Guizhoupecten* is widely distributed in the Permian, above the Wolfcampian equivalents, of the Northern Hemisphere. A Yugoslav shell from the Upper Carboniferous described as *Acanthopecten*? *orientalis* somewhat resembles *Guizhoupecten* but the morphology better suggests *Streblochondria* (Astafieva-Urbaitis and Ramovs, 1978).

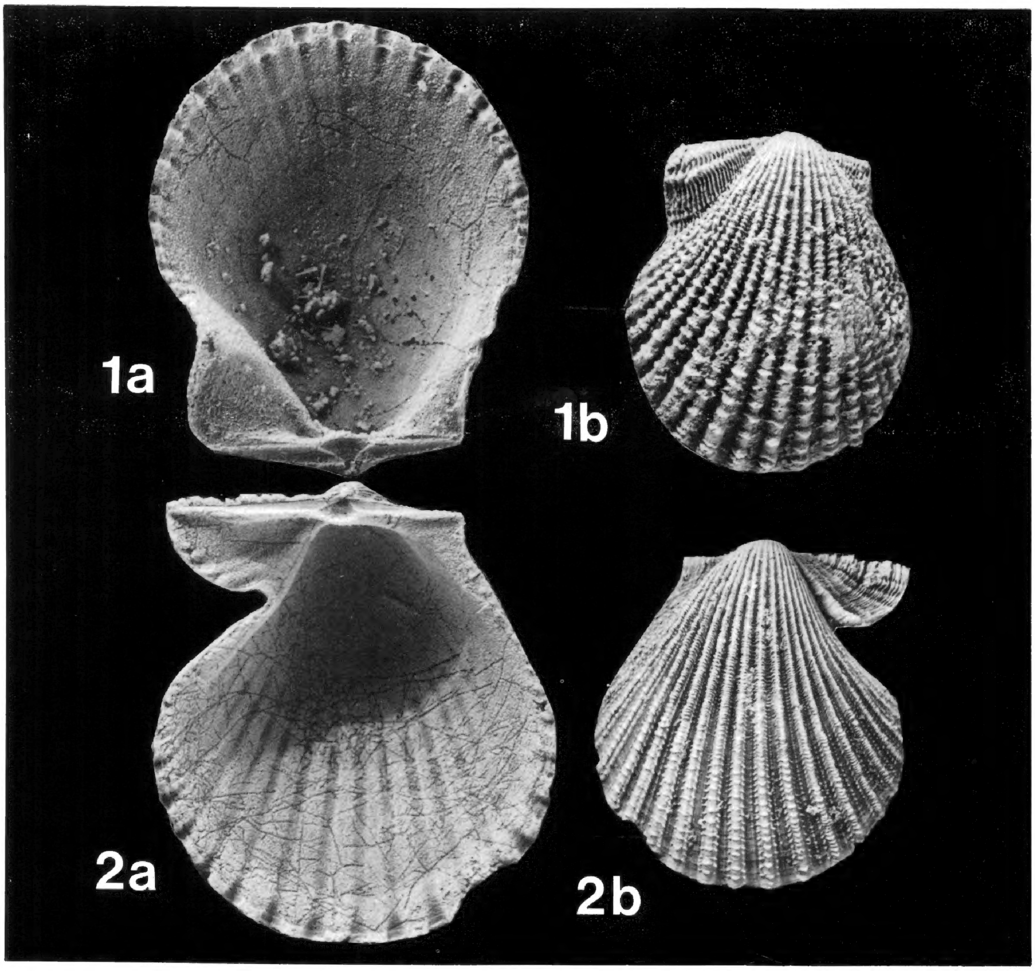

FIG. 4. *Guizhoupecten cheni,* Newell and Boyd, new species. Illustrating hinge and plicated margin. **1a.** Left valve, the holotype, ×5, with well-defined single cardinal crus on each side, broad ligament interarea, and triangular resilifer. **1b.** Exterior of the same, × 3. **2a.** Right valve, ×5, with corresponding rather obscure crus along edge of hinge plate. **2b.** Exterior of same, ×3. 1 and 2 are from two associated animals, not from a single individual. AMNH loc. 512; 1a and 1b, the holotype: AMNH cat. no. 42884; 2a and 2b: AMNH cat. no. 42885.

Guizhoupecten cheni, Newell and Boyd, new species
Figures 3–13, tables 2–6

?*Aviculopecten guadalupensis* Girty, 1908, p. 436, pl. 16, figs. 20, 20a.
?*Aviculopecten* sp. *a* Girty, 1908, p. 436, pl. 16, fig. 21.
Streblochondria guadalupensis Ciriacks, 1963, p. 53, pl. 8, fig. 8.

The new species is named for Dr. Chen Chu-zhen (Chen Chu-Chen) of the Nanjing Institute of Geology and Paleontology, Academia Sinica, author of the Genus *Guizhoupecten.*

DIAGNOSIS: Upright shells with predominantly downward (infracrescentic, acline) gradient; mean height/length ratio about 1.2/1, ranging upward in size to a maximum observed length of 66 mm (fig. 9); hingeline short, about 60–70 percent of the shell length.

Plications (fig. 4) range in number from 12 to 23, inclusive, with the most frequent number around 17 and 18 (table 2); additional

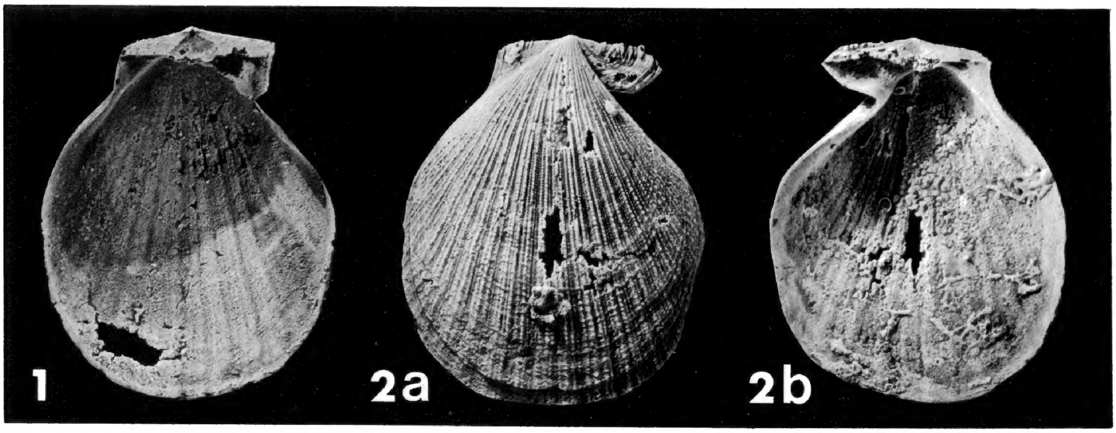

FIG. 5. *Guizhoupecten cheni,* Newell and Boyd, new species. Matched valves of a mature individual showing obsolescence of the marginal plications, an unusual feature in the collections. Natural size. **1.** Left valve, cat. no. USNM 382769. **2.** Right valve, cat. no. USNM 382770. Lamar Limestone Member, Bell Canyon Formation, Uppermost Guadalupian, West Texas, the youngest representative of *Guizhoupecten* in North America. USNM loc. 728p.

costellae usually also present; umbonal angle 58–86° with the mode around 70–75°; convexity in both valves relatively great for Paleozoic pectinoids, averaging about 42 percent of shell height in left valves and 32 percent in right valves.

MATERIAL: The hypodigm before us consists of a large number of siliceous pseudomorphs, belonging mainly to small, separated, and fragmentary juveniles generally less than 20 mm high when restored. There are only nine valves greater than 4 cm high, eight of them right valves. The largest is an incomplete right valve estimated at an original height of about 7.1 cm (fig. 9). In most specimens the inner layer, including the hinge, is missing, having been differentially leached away before silicification. The small, separated, and generally broken valves suggest winnowing and mixing of the material before burial.

TABLE 2
Composite Frequency of Main Ribs of *Guizhoupecten cheni,* New Species[a]

Main Ribs (no.)	Frequency
12	1
13	7
14	5
15	23
16	28
17	39
18	39
19	25
20	17
21	11
22	8
23	1
	204 specimens

[a] Approximately equal numbers of right and left valves are combined from localities 512 and 706e.

DESCRIPTION: Strong interlocking plications are characteristic of the disk margins (ranging in number from 12 to 23), with the most frequent number of 17 or 18 in 38 percent of the specimens. Externally, the principal ribs first appear on the beaks at a shell height of around 3 mm. They usually bear fine costellae which vary considerably in prominence and number, and are distributed randomly in the slopes and in the troughs between the main ribs. There is some uncertainty about marginal crenulations in the largest specimens, since the disk rim is preserved in only one individual (fig. 5). In this specimen, externally like *G. cheni,* the plications apparently become obsolete late in ontogeny.

The plications are pronounced only at the shell margin, and they tend to die out or be broken away toward the auricles, so that the exact number cannot always be ascertained. Consequently, the plications were again

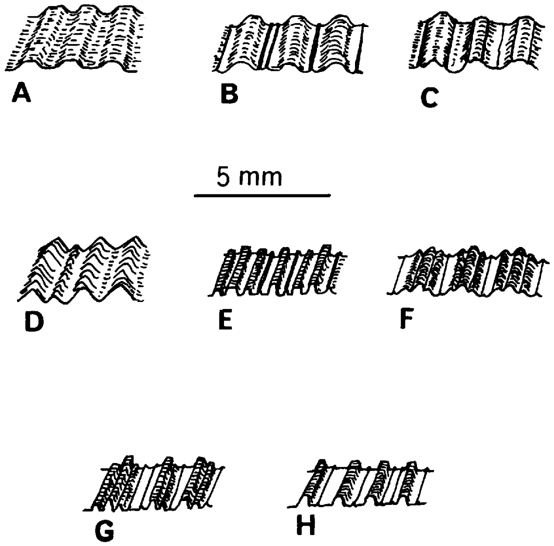

FIG. 6. *Guizhoupecten cheni,* Newell and Boyd, new species. Variation in surface features. The diagrams show broad overlap of populations.

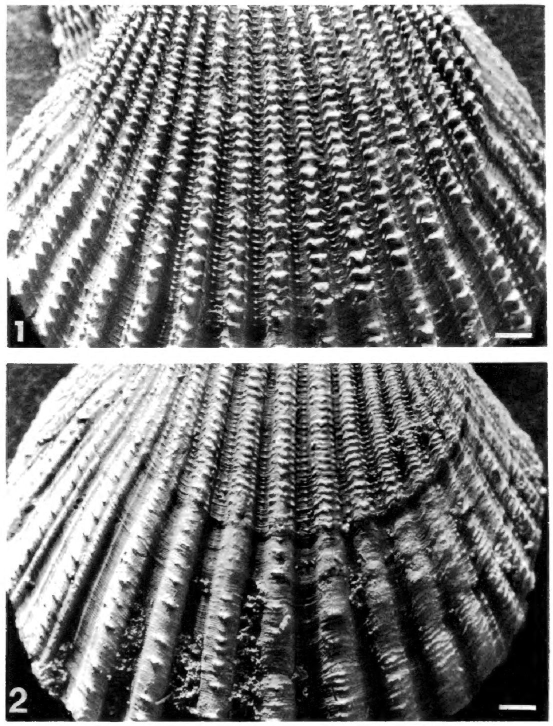

FIG. 7. *Guizhoupecten cheni cheni,* Newell and Boyd, new species and subspecies. Illustrating ornamentation. **1.** Left valve, AMNH cat. no. 42878. **2.** Right valve, displaying aberrant interruption of scales. AMNH cat. no. 42879. Both from Lower Getaway Limestone, Middle Guadalupian, West Texas, AMNH loc. 512. Scale bar is 2 mm.

counted within an arbitrary arc of 50° across the middle of the shell disk, where the number varies from about 7 to 17, with a most frequent count of 12.

During growth, plications in right valves may be added early by branching, and in the left by intercalation in the troughs. New costellae are added by intercalation, especially in left valves, but they also are added in both valves by branching, usually tangentially, along flanks of plications.

Shells with relatively broad plications tend to have narrow troughs with few, if any, secondarily added plications. In these forms, inconspicuous costellae lie along plication flanks, giving them a terraced effect (fig. 6). By contrast, a few shells with narrow plicae have variable costellae implanted between diverging plications. Where costellae originate along the margins of plications, they tend to migrate during growth into a median position in the troughs.

Scales: Fine, erect scales decorate all but the finest ribs of some valves (fig. 7). They may be uniformly developed over the shell disk, present only on parts of it, or absent. The spacing of the scales usually increases gradually toward the shell periphery from about 0.20 mm at shell height 5 mm, to 0.45 mm at shell height 10 mm. In one well-preserved left valve, scales were spaced 6 to 8 growth lines apart where the increments are broad, and 14 to 16 growth lines apart where the lines are crowded.

VARIABILITY: The ornamentation is highly variable and any arbitrarily designated patterns overlap and blend. In an attempt to analyze the ornamentation, we divided specimens into classes (fig. 8).

In the first of these, class I (fig. 8.1), the plications are relatively smooth and slightly broader than high. A second pattern, class II (figs. 8.5, 8.6), has erect scales on the coarser radial ridges. A third, class III (fig. 8.4), has subordinate ranks of costellae and the ridges are about as high as they are wide. These classes are joined by intermediates at well-represented localities (figs. 8.2, 8.3).

We tabulated the relative frequency of these

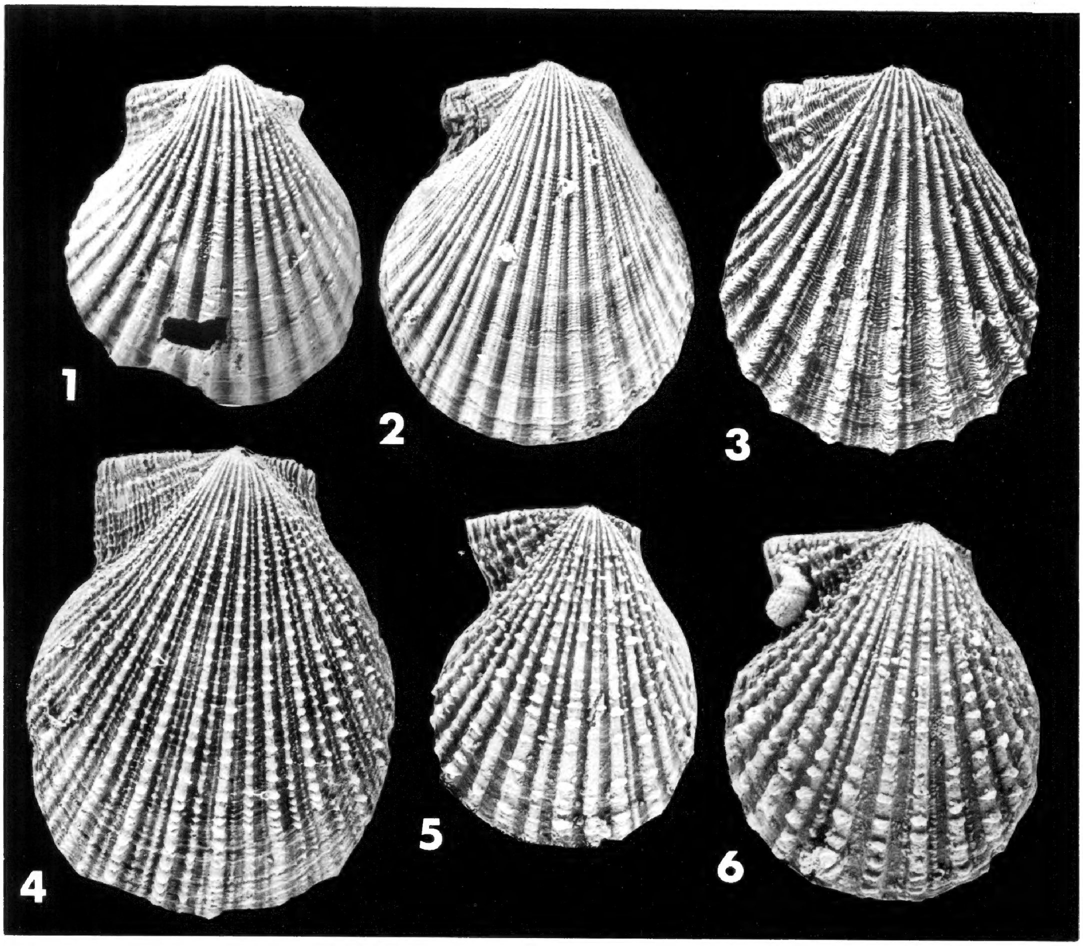

FIG. 8. *Guizhoupecten cheni willisensis,* new subspecies. Illustrating marked variability in a single population. Middle Guadalupian, Willis Ranch Member, Word Formation, West Texas. **1-6.** USNM loc. 706e, cat. nos. (respectively) 382771–382776. All left valves, ×2.

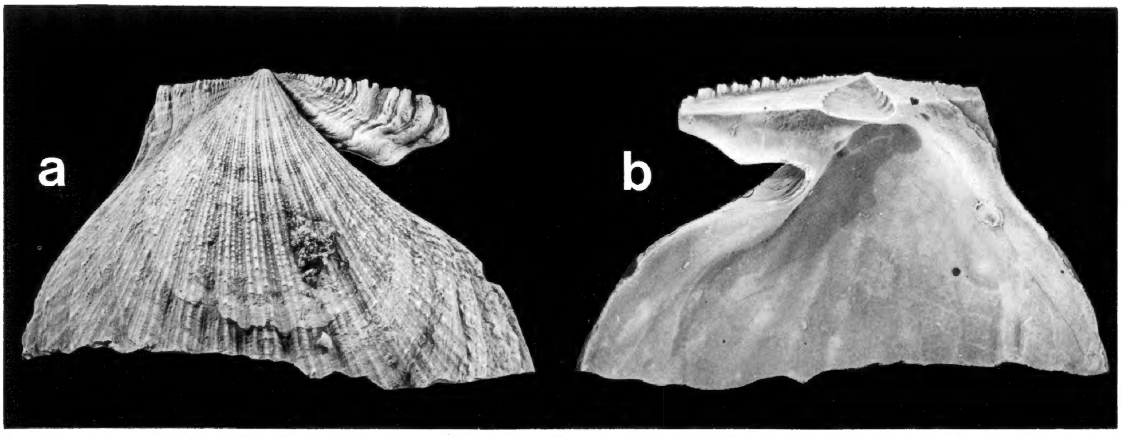

FIG. 9. *Guizhoupecten cheni,* Newell and Boyd, new species. This is the largest known representative of *Guizhoupecten,* a right valve, natural size. Lower Getaway Limestone, Middle Guadalupian, West Texas. AMNH cat. no. 42877. AMNH loc. 512.

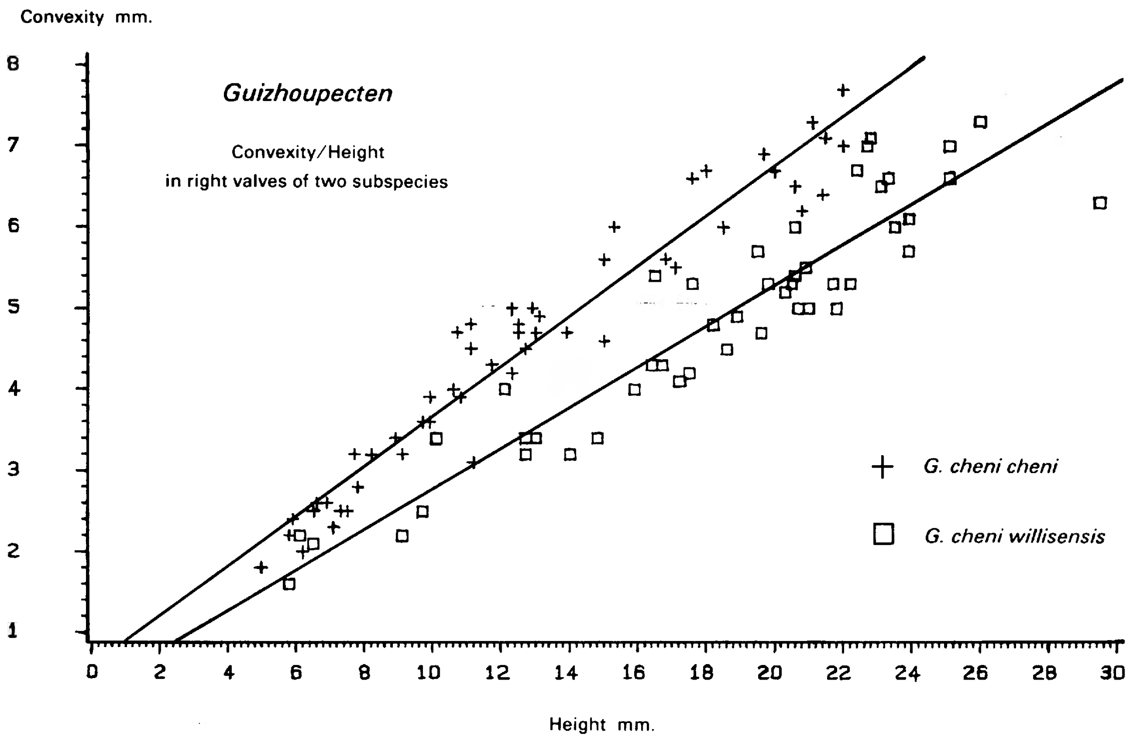

FIG. 10. Comparison of convexity of right valves in subspecies of *Guizhoupecten cheni,* new species. The two samples are about the same age, geologically, but from separate localities: *G. cheni cheni,* AMNH loc. 512; *G. cheni willisensis,* USNM 702e.

arbitrary classes in left valves at all the better represented localities (ten or more individuals). The result was that 12 or 13 localities had random representatives of two or all three of the classes plus intermediates.

There is a hint, however, of a slight upward trend for replacement of class III by class I, but we were unable to document this convincingly. Combining all our data gave the following results: Class I is rare in Leonardian samples and abundant in the lower Guadalupian. Class III is abundant in the Leonardian and rare in the lower Guadalupian. Class II is common throughout. The Capitanian horizons are too poorly represented for generalization.

In another test of possible distinctive geographic and stratigraphic patterns of ornamentation, 500 specimens were distributed by locality samples into arbitrary classes as shown in figure 6.

Each class was based on rib profiles over the central part of the disk at an ontogenetic height of 15 mm. We could not recognize normal distributions of the variants. The complex intergradation of patterns was a continual reminder of the artificial nature of the categories.

Mature specimens are rare in our collections. Nine shells more than 40 mm high are scattered through the Guadalupian sequence; all but one of these are right valves. They all exhibit the bundled pattern of ribs of figures 3, 5, and 9.

SUBSPECIES: Large samples (more than 100 specimens) from a single stratigraphic level (middle Guadalupian), at two localities 150 miles apart around the rim of the Texas Delaware Basin, seem to be taxonomically distinct although not separable in small samples (figs. 10, 11). They are treated here as ecological subspecies. All of our samples display mechanical mixing expected of reef-flank debris. In situ reef specimens were poorly preserved and not useable.

One of the samples (Lower Getaway, AMNH loc. 512) is taken as the typical population of a subspecies, *Guizhoupecten cheni*

TABLE 3[a]
***Guizhoupecten cheni cheni,* New Subspecies**

RIGHT VALVES AMNH loc. 512, N = 51			
	Mean	Range	S.D.[b]
L	10.6	16.1	4.6
H	12.0	17.0	5.0
C	4.5	5.9	1.6
Hi	7.6	9.8	2.7
A	4.6	5.7	1.6
P	2.9	4.2	1.1
U	69.2	18.0	4.7
R	17.7	18.0	1.4
	Intercept	Slope	Variance
H/L	1.07 ± 0.14	1.09 ± 0.12	0.16
C/H	0.59 ± 0.15	0.31 ± 0.01	0.16
Hi/L	1.52 ± 0.19	0.57 ± 0.02	0.31
A/P	0.72 ± 0.12	1.33 ± 0.06	0.26

[a] Explanation for tables 3–6: L, length; H, height; C, convexity; Hi, hinge length; U, umbonal angle; A, anterior ear; P, posterior ear; R, rib count. Linear measurements in mm.
[b] Standard deviation.

cheni. It is characterized by slightly rounder and more convex shells, shorter anterior ear, and, in a majority of specimens, by less conspicuous or absent costellae (fig. 4). Our class I (fig. 8) is dominant here but all the classes of ornamentation are represented.

TABLE 4
***Guizhoupecten cheni cheni,* New Subspecies**

LEFT VALVES AMNH loc. 512, N = 50			
	Mean	Range	S.D.[a]
L	12.3	19.7	4.3
H	14.6	23.7	5.0
C	5.2	6.6	1.5
Hi	8.5	12.1	2.6
A	5.1	6.6	1.6
P	3.4	5.5	1.1
U	75.2	12.0	2.7
R	18.6	9.0	2.2
	Intercept	Slope	Variance
H/L	0.35 ± 0.17	1.16 ± 0.13	0.15
C/H	1.25 ± 0.24	0.27 ± 0.16	0.30
Hi/L	1.25 ± 0.25	0.59 ± 0.02	0.34
A/P	0.61 ± 0.29	1.33 ± 0.08	0.39

[a] Standard deviation.

TABLE 5
***Guizhoupecten cheni willisensis,* New Subspecies**

RIGHT VALVES USNM loc. 706e, N = 47				
	Mean	Range	Sample Size	S.D.[a]
L	14.8	18.7	46	4.53
H	18.24	23.7	46	5.45
C	4.8	5.7	46	1.46
Hi	7.8	7.5	9	2.76
A	5.1	5.2	9	1.86
P	2.7	2.8	9	0.97
U	74.5	28.0	46	5.99
R	17.7	10.0	46	2.11
	Intercept		Slope	Variance
H/L	0.57 ± 0.29		1.20 ± 0.02	0.34
C/H	0.29 ± 0.27		0.25 ± 0.01	0.29
Hi/L	1.40 ± 0.70		0.56 ± 0.06	0.60
A/P	0.44 ± 0.96		1.70 ± 0.33	0.84

[a] Standard deviation.

The other new subspecies, *G. cheni willisensis,* is based on a hypodigm from the Willis Ranch member of the Word Formation (USNM loc. 706e); it is scalier and more ovate (fig. 8). The holotype (fig. 8.4) represents the dominant variant here. The most consistent difference from the Getaway population, however, is the slightly flatter convexity of

TABLE 6
***Guizhoupecten cheni willisensis,* New Subspecies**

LEFT VALVES USNM loc. 706e, N = 50			
	Mean	Range	S.D.[a]
L	13.3	15.0	3.84
H	16.4	17.7	4.62
C	5.1	4.9	1.27
Hi	9.1	11.1	2.57
A	5.8	7.6	1.72
P	3.2	4.3	0.93
U	74.6	18.0	3.91
R	16.1	9.0	2.08
	Intercept	Slope	Variance
H/L	0.53 ± 0.27	1.19 ± 0.02	0.28
C/H	0.78 ± 0.20	0.26 ± 0.01	0.15
Hi/L	0.56 ± 0.38	0.64 ± 0.30	0.55
A/P	0.67 ± 0.45	1.60 ± 0.13	0.77

[a] Standard deviation.

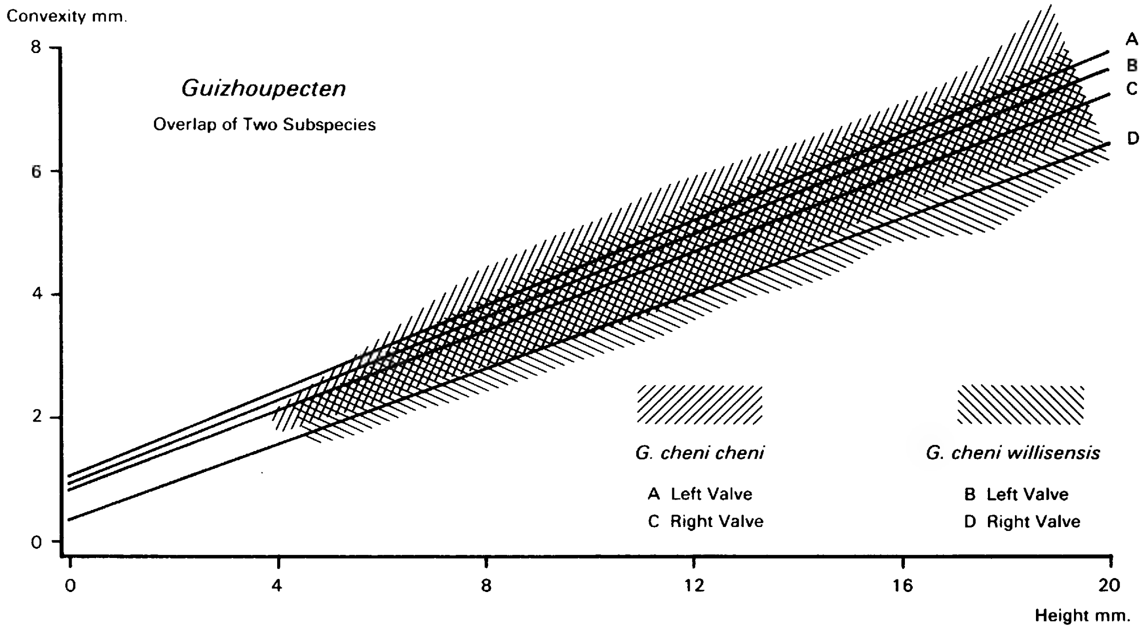

FIG. 11. Comparison of convexity of both valves in subspecies of *Guizhoupecten cheni*. Population overlap is greatest in left valves, which are nearly indistinguishable. Localities and samples as in figure 10.

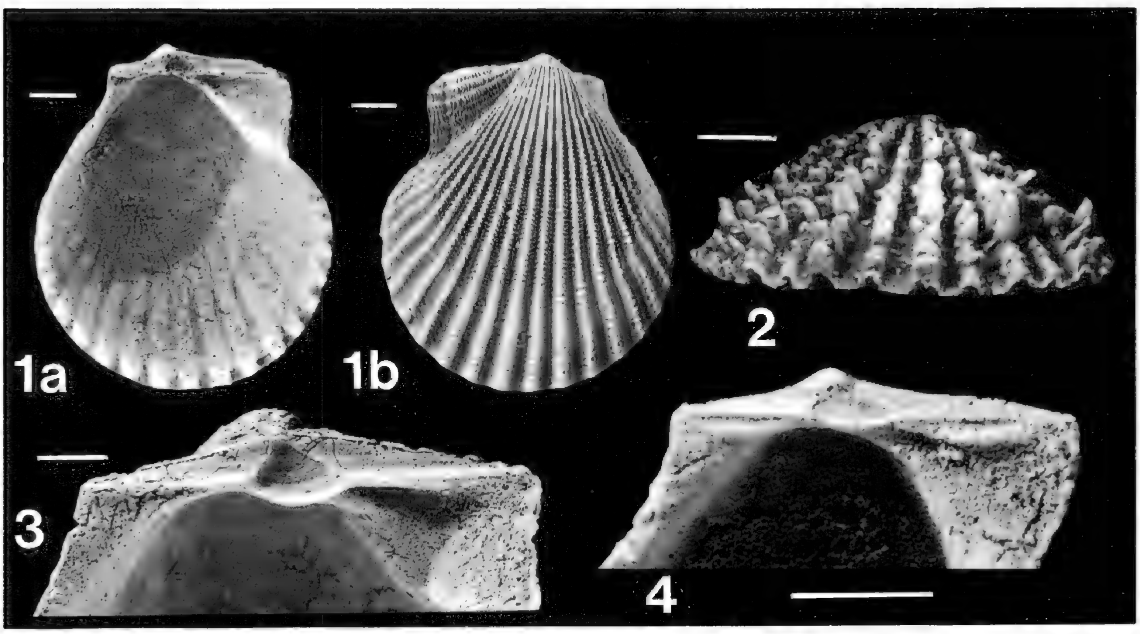

FIG. 12. *Guizhoupecten cheni cheni,* Newell and Boyd, new species and subspecies. Illustrating morphological details. Lower Getaway Limestone, Lower Guadalupian, West Texas, AMNH loc. 512. **1.** The holotype, a left valve. AMNH cat. no. 42880. **2.** Marginal view of a left valve. AMNH cat. no. 42881. **3.** Hinge details, left valve. AMNH cat. no. 42882. **4.** Cardinal crus of juvenile. AMNH cat. no. 42883. The scale bars represent 2 mm.

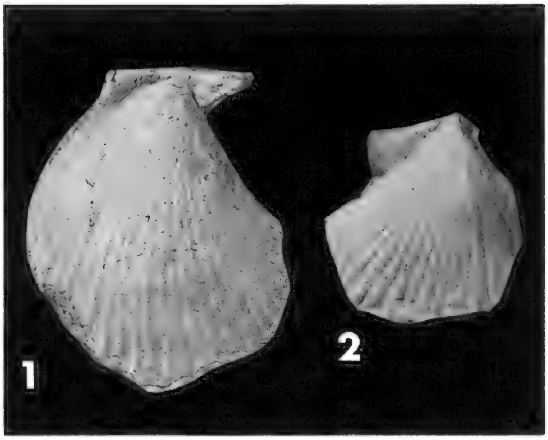

FIG. 13. *Guizhoupecten* species. G. H. Girty's 1908 originals from USGS loc. 2930, Capitan, Guadalupe Mountains, West Texas (Capitan Fm., probably Pinery member). **1.** Right valve, ×2. USNM cat. no. 118237. Published as *Aviculopecten* sp. *a*. **2.** *Aviculopecten guadalupensis* Girty, the holotype, ×2. USNM cat. no. 118236. This is too imperfect to be recognizable.

the right valve in *G. cheni willisensis* (figs. 10, 11).

Individuals displaying some of the characteristics of both populations occur together at various stratigraphic levels in the Leonardian and Guadalupian limestones of western Texas. Our purpose in naming the two populations is to stress their obscure, but real, statistical differences, which most likely reflect different microhabitats, rather than geographic isolation.

Right and left valves in Pectinacea are sufficiently unalike that they have to be analyzed separately; therefore, the statistics of the two valves in each of the two populations have been treated separately.

COMPARISONS: Two bivalves described by Girty (1908) as *Aviculopecten guadalupensis* and *Aviculopecten* sp. (fig. 13) probably belong to *Guizhoupecten*. They were collected in the Pinery Limestone of mid-Capitanian age. Both may be conspecific with *G. cheni*, but this is only a guess, and the specimens are so poorly preserved that they are specifically unidentifiable.

For the same reason, it is difficult to discriminate our new species from some previously named species of *Guizhoupecten*. Consequently, the following comparisons are only suggestive.

The type species of the genus, *G. wangi* Chen, 1962 and *G. regularis* Chen, 1962 both have coarse, uncrowded ribs alternating in size, and the umbonal angle seems to be greater than the average for *G. cheni*.

A Wyoming shell described by Ciriacks (1963) from the Park City Formation as *Streblochondria*? *guadalupensis* is probably a representative of *G. cheni*, but his species *Streblochondria*? *tubicostata* has more numerous and narrower plications than the average for *G. cheni*.

A Greenland species of *Guizhoupecten* about the same age (Guadalupian) as the Texas species was described by Newell (1955) as *Streblochondria*? *maynci*. It is considerably less convex than *G. cheni* and has a greater umbonal angle.

SUMMARY

Representatives of the Streblochondriidae are cosmopolitan in the Upper Paleozoic of the Northern Hemisphere. But until the present study, the documentation had been based on inadequate and poorly preserved samples. The exceptional abundance of well-preserved material in our Texas collections has enabled us to document both morphology and population variability for the first time, and should now provide a world standard for this family. The marked variation of these fossils underlines the importance of revising the heretofore named species on ample population samples.

We have elevated this group from subfamily to family status because of the combination of characters that distinguish it from most Upper Paleozoic scallops: procrescentic (opisthocline) form, subequal convexity of valves, and the fibrous outer layer in both valves.

The most advanced genus, *Guizhoupecten*, resembles post-Paleozoic scallops in its possession of plications and the presence of previously unknown cardinal crura in juveniles. The ligament complex is primitive, suggesting that the family is morphologically intermediate between Carboniferous Aviculopectinidae and Triassic Pectinidae, which are

separated by the great episode of mass extinction.

Parallel evolution is so prevalent in pelecypods (Newell and Boyd, 1975) that we withhold phylogenetic judgment until we have been able to study adequately the dozens of other scallop genera of the Permo-Triassic.

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